

# CTENOPHORUS TJANTJALKA, A NEW DRAGON LIZARD (LACERTILIA: AGAMIDAE) FROM NORTHERN SOUTH AUSTRALIA

G. R. JOHNSTON

JOHNSTON, G. R. 1992. *Ctenophorus tjantjalka*, a new dragon lizard (Lacertilia: Agamidae) from northern South Australia. *Rec. S. Aust. Mus.* 26(1): 51-59.

A new species of agamid lizard, *Ctenophorus tjantjalka*, is described and illustrated. It is saxicolous in habit, appears to be confined to northern South Australia and is a member of the *C. decresii* species group. It may be distinguished from all other members of this group by its deep head and short snout, wrinkled snout scales, the presence of a vertebral keel, dorsal colouration of males and females and the lack of banding on the tail.

Greg Johnston, Department of Anatomy and Histology, University of Adelaide, GPO Box 498, Adelaide, South Australia 5001. Present Address: School of Biological Sciences, Flinders University of South Australia, Bedford Park, South Australia 5042. Manuscript received 28 October 1991.

Members of the *Ctenophorus decresii* species group represent a distinct saxicolous ecomorph within the extensive Australian radiation of agamid lizards. This group has been diagnosed by Houston (1974) and extended by Storr (1981). The species described herein as new, is a member of the *C. decresii* species group and inhabits the barren, rocky ranges of far northern South Australia.

Specimens of this taxon have been received at the South Australian Museum since 1960 but were variously misidentified, most of them as either *C. rufescens* or *C. vadrappa*. Warburg's (1966) reference to *C. fionni* at Wintinna in northern South Australia was probably based on this species. White's (1979) records of *C. vadrappa* from the Mabel Range near Oodnadatta are also based on this species. Houston (1978) regarded several specimens of this new species as *C. rufescens*, thereby incorrectly extending that species' distribution east of the Stuart Highway.

## MATERIALS AND METHODS

Eighteen morphometric measurements and eight meristic counts were made of all available specimens of the new taxon ( $N = 17$ ) and *C. rufescens* ( $N = 89$ ), and a selection of *C. vadrappa* ( $N = 42$ ) in the South Australian Museum (SAM) and Western Australian Museum (WAM). Morphometric measurements were snout-vent length (SVL), the distance between the tip of the snout and the anterior margin of the eye (SL), eye diameter (EYE), the horizontal distance from the posterior margin of the eye to the angle of the jaw (POCL), head depth immediately behind the eye (HD), width between the nostrils (SWD), width between the tympani (HWD), length of the upper arm (HUML), length of lower arm (FAL), length of the hand (ML), length of the thigh (FEML), length of tibia (TIBL), length of foot (PL), distance from axilla to groin (AG),

tail length (TL), head length (HL = SL+EYE+POCL), forelimb length (FLL = HUML+FAL+ML) and hindlimb length (HLL = FEML+TIBL+PL). Meristic counts were the number of scales between the rostral and the nasal (PRENAS), number of scales between the nasal and the supralabials (SUBNAS), number of scales between the nasals across the top of the snout (INTERNAS), number of supralabials (SUPLAB), number of infralabials (INLAB), number of subdigital lamellae on the fourth finger (SD4F), number of subdigital lamellae on fourth toe (SD4T) and the number of femoral and preanal pores (FEMPREPO).

Descriptive statistics were calculated for a number of meristic characteristics (Table 1) from samples of *C. rufescens*, *C. vadrappa* and the new taxon. Multiple comparisons of these variables were made using single classification ANOVA (Sokal & Rohlf 1981). Multiple discriminant function analyses (Reyment *et al.* 1984) of raw measurements and meristic characteristics were done using SPSS PC+ (Norusis 1986) on a Pantek PC-16 personal computer. Sexes were pooled for all analyses.

Ontogenetic variation was examined by fitting HL, HD, HWD, FLL, FEML, ML, HLL, TL and SVL for *C. rufescens*, *C. vadrappa* and the new taxon to the logarithmic form of the allometric equation  $Y = bSVL^a$  (Huxley 1932; Gould 1966), where Y is the variable being examined, SVL is used as a measure of overall size,  $a$  is the allometric coefficient (slope) and  $b$  is the y-intercept. Allometric coefficients were tested against unity using standard normal deviates (Zar 1974).

*Ctenophorus tjantjalka* sp. nov.

Figs 1-3, 5B

*Types*

Holotype: SAM R17934a just N Mabel Range, S.

Aust., 26°45'S, 113°48'E, South Australian Herpetology Group, 18-20.iv.1979, male.

Paratypes: SAM R4328 Mt Chandler, S. Aust. (27°00'S, 113°19'E), H. Wopfner, 20.x.1960; SAM R6227 80 miles W Oodnadatta, Copper Hill Station (27°57'S, 134°19'E), H. Frahn, 19.vii.1965; SAM R12495 20 miles S Hawks Nest Well, S. Aust. (27°45'S, 134°07'E), J. Bredl, 1971; SAM R15608 Rocky Gully, SW old Peake HS, S. Aust. (28°05'S, 135°54'E), Rostrevor College, ix.1976; SAM R15936a-d near Peake Ruins, S. Aust. (28°05'S, 135°54'E), T. F. Houston, 18-19.iv.1977 (SAM R15936a is a dried skeleton); SAM R17701 Hawks Nest Well, S. Aust. (27°30'S, 134°13'E), B. Miller and M. Galliford, 26.iii.1979; SAM R17934b, SAM R17935 just N Mabel Range, S. Aust. (26°45'S, 135°48'E), South Australian Herpetology Group, 18-20.iv.1979; SAM R20579-80 Copper Hill Station, 19km E Mt Willoughby, S. Aust. (27°57'S, 134°19'E), D. J. Morafka, 12.iv.1979; SAM R36731-33 Davenport Range, S. Aust. (28°27'S, 136°02'E), M. Adams and T. Reardon; SAM R37115 83km N Coober Pedy, S. Aust. (28°27'S, 134°12'E), J. Cornish, 15.x.1990.

#### Diagnosis

A member of the *Ctenophorus decresii* group (*sensu*

Houston 1974 and 1978, *cf.* Storr, Smith & Johnstone 1983). Distinguishable from all other members of this group in the following combination of characters: snout scales wrinkled; vertebral keel line present, at least anteriorly; flanks with pale cream to pale salmon pink patches on a grey-brown background in adult males; large pale grey to white spots present on dorsum in females and juveniles; tail without broad alternate dark and pale bands.

#### Description

A robust, moderate-sized dragon lizard reaching a SVL of 73 mm and a total length of 208 mm; head relatively short and deep; snout moderately obtuse, rising fairly steeply in profile; nostril below a sharp canthus rostralis; body moderately depressed; forelimbs relatively large, reaching or almost reaching groin when adpressed; hindlimbs quite long, 94-122 percent of SVL; tail long and evenly tapering. In juveniles the head and appendages are relatively longer than in adults (Table 2).

Scales on top of snout coarsely wrinkled in adults, tending to simple keeled in juveniles; a row of enlarged, longitudinally-ridged or carinate scales from nostril below eye to above ear; outer margins of eyelids fringed with a row of acute scales; 5-7 scale rows separating



FIGURE 1. Adult male *Ctenophorus tjantjalka* (SAM R36731) from the Davenport Range, South Australia. SVL = 65mm.



FIGURE 2. Adult female *Ctenophorus tjantjalka* (SAM R37115) from 83km N Coober Pedy, South Australia. SVL = 47mm.

nasals from supralabials; 13-17 supralabial scales on each side; temporal, occipital, nuchal and axillary scales generally very small and convex; folds of skin above and behind ear opening on sides of neck with clusters of small spines, feebly developed in juveniles; low nuchal crest present; a row of perfectly aligned, keeled scales extends dorsally from the nuchal crest to the base of tail along the midline in males, may be feebly developed in females and juveniles; this keel line frequently accentuated by being raised on a fold of skin; scales on flanks small, subtubercular and homogeneous, grading into slightly larger, flatter dorsal body scales which are feebly keeled in adults to smooth in some juveniles; flanks without scattered individual tubercles; ventral scales homogeneous, smooth, substantially larger than dorsal scales and much larger than lateral scales; scales on tail and dorsal surfaces of limbs large and strongly keeled; 33-46 femoral and preanal pores regularly spaced, with 1-4 scales between pores, along a more or less straight line extending the full length of thighs, but interrupted medially; each pore surrounded by several scales, those anterior to it being slightly enlarged.

Adult males (Fig. 1) vary from dark, chocolate brown to grey dorsally, with dark grey to black reticulations which tend to form an irregular

dorsolateral stripe. Paler reticulations tend to form transverse bars on flanks which interrupt dark dorsolateral stripes; these pale bars are pale cream dorsally, grading to pale salmon pink laterally. Vertebral region brown to grey, peppered with black and cream, as are the tail and limbs; tail may have irregular darker and lighter bands distally. Chest and ventral surface of forelimbs dark grey to black, tapering toward the midline caudally. Gular fold and clusters of spines on nape pale cream. Bars of grey to brown and cream radiate from the eye to the brow, and from the eye over the upper lip, and along the lower lip. Throat cream with fine, dark grey reticulations, tending to form 2-3 irregular stripes on jowls. Scapular fold black with cream edge.

Adult females (Fig. 2) brick-red to brown dorsally; cream ventrally. Irregular black transverse bars on flanks, interspersed with thinner irregular pale grey white bars. Vertebral region with irregular black and pale grey spots which may align and be continuous with lateral bars. Dorsal surfaces of limbs peppered with pale grey scales and irregular, small, black markings. Throat and chest lightly peppered with dark grey to black, becoming heavier on jowls where it tends to form 2-3 irregular stripes. Clusters of spines on nuchal region pale grey to white.

Juveniles are very similar to the females in colour and pattern; the pattern may be finer than in adults. Specimens which have been in alcohol for some time fade considerably so that the dorsum becomes pale brown and any pattern barely visible.

#### *Measurements of Holotype* (in mm)

Snout-vent length, 73.0; head length, 15.5; head width, 15.2; fore limb length, 33.3; hind limb length, 78.1; tail length, 135.

#### *Etymology*

The specific epithet is the name used by the Aboriginal people of north-western South Australia for saxicolous agamid lizards. It is used as a noun and is not subject to termination changes.

#### **Distribution and Habitat**

Widespread in the interior of South Australia, between the Indulkana Range and Oodnadatta in the north and Coober Pedy and the Davenport Range in the south (Fig. 3).

All specimens of *C. tjantjalka*, for which information is available on habitat, were collected in or among rocky outcrops. SAM R12495 was collected 'on granite outcrops'. SAM R15936a-d was collected 'in small granite outcrops in gullies' and SAM R17701 was 'active

on outcrops'. White (1979) collected specimens (SAM R17934a-b, SAM R17935) '... on mid to lower slopes of gibber strewn hills...' John Cornish (pers. comm. 1990) collected SAM R37115 under gibber rocks in a slight gully.

#### **Comparison with Similar Species**

##### *Morphology*

*C. tjantjalka* is clearly a member of the *C. decresii* species group (Houston 1974, 1978) in being of moderate size with head and body moderately to strongly depressed, showing sexual dimorphism and being of saxicoline habit. It differs from *C. ornatus* and *C. yinnietharra* in lacking extreme depression of the head and body, and having no clear broad bands of colour around the tail in males. Similarly, the head and body of *C. tjantjalka* are less depressed than those of *C. decresii*, *C. fionni*, *C. rufescens* and *C. vadrappa*. The presence of pale spots (in females) or reticulations (in males) on the dorsum distinguishes *C. tjantjalka* from *C. rufescens*, as does the lower number of femoral and preanal pores (Table 1). The snout scales of *C. tjantjalka* are consistently wrinkled, as in *C. vadrappa* (Houston 1974), which serves to distinguish it from *C. decresii* and most *C. fionni*. Male *C. tjantjalka* have pale cream to pale salmon pink areas on the flanks, as opposed to the red or orange areas

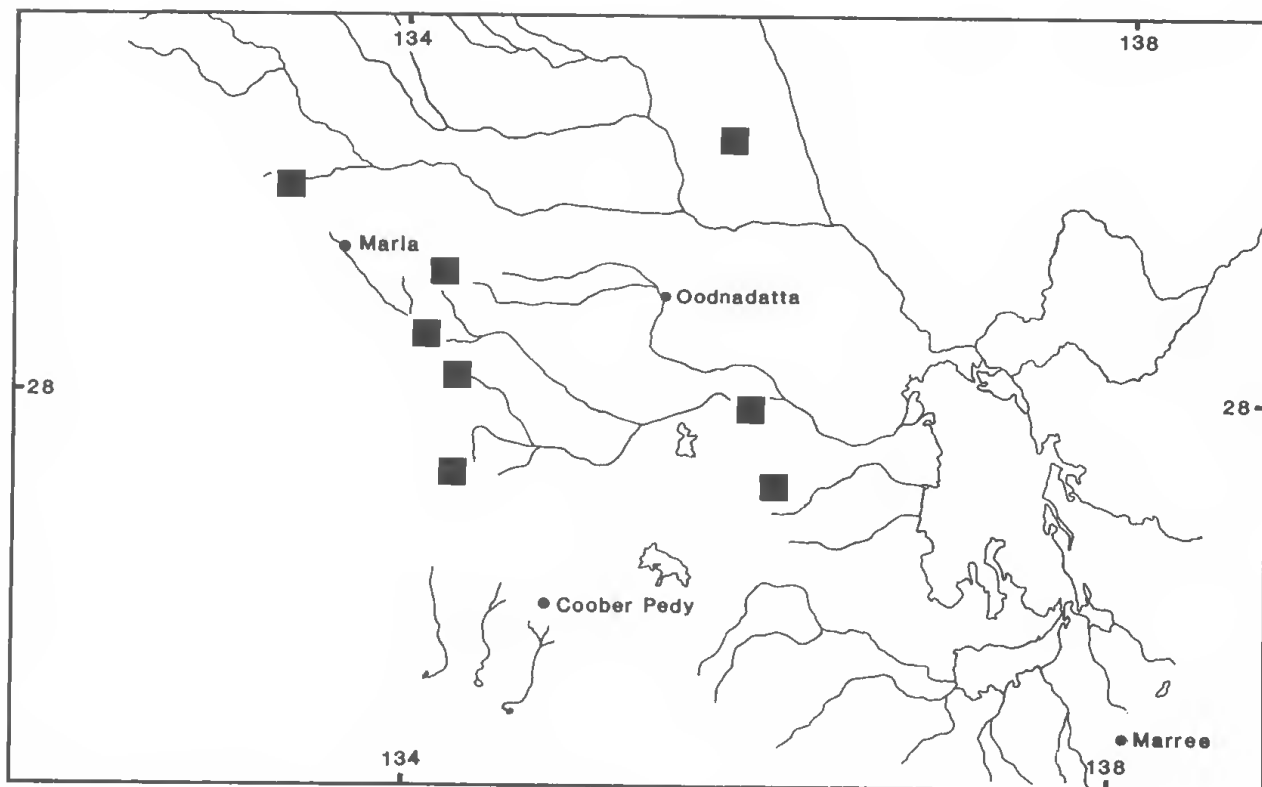


FIGURE 3. Map of northern South Australia showing localities (■) from which *Ctenophorus tjantjalka* has been collected.

on the flanks of male *C. vadrappa*. Male *C. vadrappa* are further distinguished from male *C. tjantjalka* in having a blue background dorsal colour when active. The background colour on the dorsum of *C. tjantjalka* is grey to brown. *C. tjantjalka* and *C. vadrappa* both have a vertebral line of keeled scales present, at least anteriorly, unlike *C. decresii* and *C. fionni* in which any keeled vertebral scales are associated with the nuchal crest only and do not extend behind the shoulders. *C. tjantjalka* lacks the tiny white spiny tubercles found on the flanks of *C. decresii*. Female *C. tjantjalka* may be distinguished from all other members of the *C. decresii* group in having large pale grey spots on the dorsum. The relatively deep head and short snout distinguish both sexes of *C. tjantjalka* from all other members of the *C. decresii* group.

Although all meristic characters counted showed statistically significant differences ( $P < 0.01$ ) between *C. tjantjalka*, *C. rufescens* and *C. vadrappa*, the actual counts for all except FEMPREPO overlapped extensively (Table 1).

Several populations of *C. caudicinctus* are similar in general morphology to members of the *C. decresii* group. This may be due to their being of similar saxicolous habit. Houston (1974) has suggested that the *C. decresii* group may share a common ancestry with some populations currently subsumed under the epithet *C. caudicinctus*. The deeper head and less depressed body of *C. tjantjalka*, relative to other members of the *C. decresii* group, are reminiscent of some populations of *C. caudicinctus*. These taxa may be distinguished by the presence of clusters of small spines on folds of skin on the nape and neck of *C. tjantjalka* which are absent or poorly developed in *C. caudicinctus*. The

forelimbs of all members of the *C. decresii* group show negative allometric growth (Table 2; Witten 1985) whereas in *C. caudicinctus* the forelimbs grow isometrically (Witten 1985).

#### Distribution

*C. tjantjalka* is allopatric to all other members of the *C. decresii* group and *C. caudicinctus*. The only species which are likely to be confused with *C. tjantjalka* on grounds of distribution are *C. rufescens* and *C. vadrappa*. Both of these species occur on rocky ranges abutting the known distribution of *C. tjantjalka*.

#### Discriminant Function Analysis

Discriminant function analysis of 15 measurements, using *C. rufescens*, *C. tjantjalka* and *C. vadrappa* as *a priori* groupings (Fig. 4), resulted in correct identification of 92.5% of specimens overall. All *C. tjantjalka*, 93.1% of *C. rufescens* and 89.8% of *C. vadrappa* were correctly grouped. FLL, HLL and HL were not included in the analysis because they failed to contribute significantly to a decrease in Wilk's lambda. A separate discriminant function analysis of eight meristic characteristics, also using *C. rufescens*, *C. tjantjalka* and *C. vadrappa* as *a priori* groupings, resulted in correct identification of 89.0% of specimens overall. All *C. rufescens*, 82.1% of *C. vadrappa* and 83.3% of *C. tjantjalka* were correctly grouped.

The first discriminant function based on measurements accounted for 78.1% of the variance. Unstandardised discriminant function coefficients and their correlations to the discriminant functions are presented in Table 3. Most characters showing the highest correlation with the first discriminant function,

TABLE 1. Comparison of meristic characters for three species of *Ctenophorus*. Values represent mean (standard deviation) over minimum-maximum.

N	<i>C. rufescens</i> 55	<i>C. tjantjalka</i> 17	<i>C. vadrappa</i> 42
FEMPREPO	54.9(2.33) 43-67	38.8(1.96) 33-46	39.7(1.98) 33-47
PRENAS	5.8(0.84) 5-7	4.9(0.85) 3-6	5.1(0.81) 3-6
SUBNAS	6.5(0.85) 5-9	6.2(0.86) 5-7	5.7(0.83) 5-6
INTRANAS	13.1(1.12) 11-17	10.2(1.22) 8-15	10.3(0.97) 8-13
SUPLAB	17.4(1.20) 13-20	18.4(1.06) 13-17	15.0(0.96) 13-16
INLAB	15.6(1.16) 12-19	16.4(1.09) 13-18	15.4(0.90) 14-17
SD4F	19.2(1.15) 16-22	16.6(1.23) 14-19	17.0(1.04) 15-19
SD4T	31.8(1.42) 26-36	28.7(1.63) 24-34	27.6(1.41) 23-33

TABLE 2. Relative growth of body parts in three species of *Ctenophorus*. Regression lines of the form  $y = bx^a$  were fitted to the data.  $R^2$  = coefficient of determination;  $N$  = sample size;  $C_{30}$  = predicted size of body part at a SVL of 30mm;  $C_{80}$  = predicted size of body part at a SVL of 80mm. Allometric coefficients were compared to isometry using standard normal deviates: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ .

	$R^2$	$a$	$b$	$N$	$C_{30}$	$C_{80}$
<i>Ctenophorus rufescens</i>						
HLvSVL	0.87	0.8150**	-0.8571	55	6.8	15.1
TLvSVL	0.76	0.9616	0.9794	49	70.1	180.0
FLLvSVL	0.79	0.8254**	-0.0261	55	16.1	36.2
HLLvSVL	0.91	0.8527**	0.6379	55	34.4	79.4
FEMLvSVL	0.82	0.9006	-0.8689	55	9.0	21.7
PLvSVL	0.86	0.7793**	0.0407	55	14.7	31.7
HWDvHL	0.89	0.8997*	0.2417	55	7.1	14.6
HDvHL	0.42	0.7984	0.0140	55	4.7	8.9
SLvHL	0.93	0.9858	-0.6017	55	3.6	8.0
<i>Ctenophorus tjantjalka</i>						
HLvSVL	0.97	0.9013*	-1.0828	19	7.3	17.6
TLvSVL	0.78	0.8951	1.1501	15	66.3	159.6
FLLvSVL	0.94	0.8379**	-0.0789	19	16.0	36.3
HLLvSVL	0.91	0.8264**	0.7705	19	35.9	80.7
FEMLvSVL	0.91	0.9615	-1.1160	19	8.6	22.1
PLvSVL	0.70	0.6874**	0.4450	19	16.1	31.7
HWDvHL	0.95	0.8813*	0.2544	19	7.4	14.5
HDvHL	0.88	1.0687	-0.5733	19	4.7	10.6
SLvHL	0.94	1.0794	-0.8771	19	3.5	8.1
<i>Ctenophorus vadrappa</i>						
HLvSVL	0.92	1.0213	-1.5968	40	6.5	17.8
TLvSVL	0.95	1.0676	0.4676	30	60.3	171.7
FLLvSVL	0.92	0.8535**	-0.1758	41	15.3	35.3
HLLvSVL	0.90	0.9424	0.1933	41	29.9	75.4
FEMLvSVL	0.98	1.0563	-1.5685	41	7.6	21.3
PLvSVL	0.76	0.8194*	-0.2254	41	13.0	28.9
HWDvHL	0.61	0.9413	0.0585	40	6.2	15.9
HDvHL	0.94	0.9671	-0.4281	40	4.0	10.6
SLvHL	0.94	0.9412	-0.5052	40	3.5	9.1

which most clearly separates *C. rufescens* from *C. tjantjalka* and *C. vadrappa*, are measurements of the limbs. Most characters showing the highest correlation with the second discriminant function, which most clearly separates *C. tjantjalka* from *C. rufescens* and *C. vadrappa*, are measurements of the head. This reflects the differences in the relative proportions of the limbs and heads of the three species (Fig. 5).

#### Allometry

Relative growth among ten body parts in *C. rufescens*, *C. tjantjalka* and *C. vadrappa* is summarised in Table 2. *C. rufescens* and *C. tjantjalka* share the same pattern of relative growth. The head and limbs show negative allometry with respect to SVL. While the head decreases in size relative to SVL, the head width also decreases in size relative to the head length. Much of the relative shortening of the

hindlimb with increasing size is accounted for by negative allometry of the foot.

In *C. vadrappa* only the forelimbs shorten with increasing SVL, while all other body parts grow isometrically. Although overall the hindlimb length grows isometrically with respect to SVL, the proportions of the hindlimb change so that the foot becomes relatively shorter with respect to the rest of the limb.

Witten (1985) has studied relative growth in the majority of species of Australian agamids, but did not have data for *C. rufescens* or *C. vadrappa*. In both of these species and *C. tjantjalka* the tail grows isometrically, whereas Witten (1985) implies that in other species of the *C. decresii* group the tail shows positive allometry. In fact Witten (1982 and pers. comm. 1991) found significant positive allometry in the tail of *C. fionni*, but in other members of the

TABLE 3. Unstandardised discriminant function coefficients (and pooled-within-groups correlations with discriminant functions) of 15 measurements of three species of saxicolous *Ctenophorus*.

Variable	Discriminant Function	
	I	II
SVL	-0.046(-0.277)	0.193(0.378)
SL	1.232(-0.083)	0.426(0.316)
EYE	0.530(-0.170)	-1.501(0.179)
POCL	1.191(0.175)	0.316(0.327)
SWD	0.032(-0.174)	0.511(0.337)
HWD	-0.101(-0.140)	-0.113(0.194)
HD	0.302(0.003)	-0.271(0.053)
HUML	-0.701(-0.377)	-0.073(0.223)
FAL	0.042(-0.226)	-0.051(0.257)
ML	0.239(-0.229)	0.226(0.344)
FEML	-0.243(-0.305)	-0.130(0.260)
TIBL	-0.039(-0.281)	-0.154(0.185)
PL	-0.060(-0.349)	-0.366(0.097)
AG	-0.009(-0.332)	-0.034(0.358)
TL	-0.023(-0.368)	0.035(0.394)
constant	1.835	0.687
% of variance	78.06	21.94

*C. decresii* group he studied, the allometric coefficient for tail length was above one but not significantly so. In *C. rufescens* and *C. tjantjalka* the hindlimb shows negative allometry, in concordance with most other Australian agamids, whereas in *C. vadrappa* the hindlimb grows isometrically. Similarly head length in *C. rufescens* and *C. tjantjalka* shows negative allometry, in common with other Australian agamids, whereas the head of *C. vadrappa* grows isometrically. In most species of Australian agamids the forelimb shows negative allometry. The negative allometry or isometry of head width and head depth relative to head length in all three species is unusual among Australian agamids, in which these measurements generally show positive allometry.

#### DISCUSSION

*Ctenophorus tjantjalka* is described as a new species primarily on the basis of the remarkable consistency of its morphology across a large geographic range. In general, members of the *C. decresii* complex are characterised by a large amount of population structuring (Gibbons & Lillywhite 1981) and consequent morphological (Houston 1974) and genetic variation (Johnston & Donnellan, unpublished data) among populations within species.

One feature of *C. tjantjalka* is its robust appearance when compared with other members of the *C. decresii* species group, which are moderately to extremely

dorsoventrally compressed. In this respect adult *C. tjantjalka* resemble juveniles of other members of the *C. decresii* group. Cogger (1961) has demonstrated that heterochronic processes are an important source of morphological variation among Australian dragon lizards. In the absence of any knowledge of the phylogenetic relationships among the various species groups within the genus *Ctenophorus* it is not possible to determine whether *C. tjantjalka* has arisen through some form of paedomorphosis, or whether it represents a more 'plesiomorphic' form and all other members of the *C. decresii* group have undergone a type of peramorphosis (Alberch *et al.* 1979). This dilemma emphasises the need for a formal phylogenetic analysis of the Australian agamid lizards.

The geographic distribution of *C. tjantjalka* lies directly between those of *C. rufescens* and *C. vadrappa*. It therefore provides evidence to support Houston's (1974) hypothesis that the ancestors of *C. decresii*, *C. fionni* and *C. vadrappa* were once distributed along the western side of Lake Eyre and may have been derived via that route from a common ancestor with *C. rufescens*, among other saxicolous dragon lizards. Gibbons & Lillywhite (1981) have suggested that the *C. decresii* species group may have been derived from a hypothetical ancestor in western Queensland via the corridor of rocky country provided by the Grey Range, Barrier Range and Olary Spur, but there seems to be little to support this alternative hypothesis.

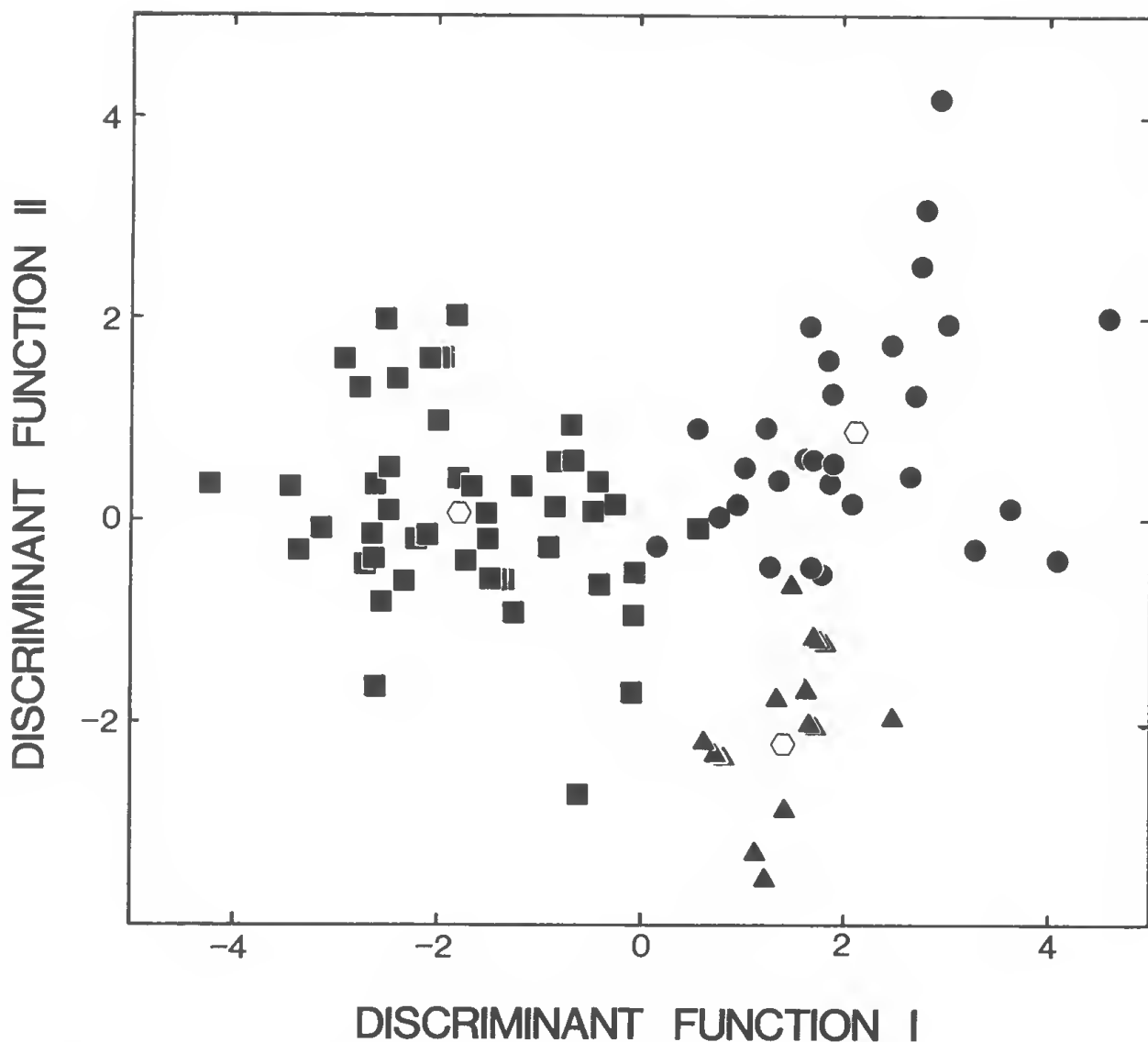


FIGURE 4. Plot of individual *Ctenophorus tjantjalka* ( $\blacktriangle$ ), *Ctenophorus rufescens* ( $\blacksquare$ ) and *C. vadrappa* ( $\bullet$ ) on the first two discriminant function axes based on fifteen morphometric characters. ( $\circ$ ) = group centroids.

### Comparative Material Examined

#### *C. rufescens*

WAM R28990-91 Pottoyu Hills (25°19'S, 129°49'E), 10.v.1967; SAM R586a-b Everard Range (27°06'S, 132°26'E), no date; SAM R586c Wantapella Swamp (27°02'S, 133°28'E), no date; SAM R1423-25 Mt Sir Thomas, Birksgate Range (27°09'S, 129°44'E), no date; SAM R3125a-c Ernabella Mission (26°18'S, 132°08'E), 10.x.1950; SAM R5632 Mann Range (26°01'S, 129°45'E), vi.1964; SAM R11754-56 Everard Range (27°06'S, 132°26'S), 1-7.xi.1970; SAM R13219 1.5 miles S Mt Illbillee, Everard Range (27°04'S, 132°29'E), 24.x.1972; SAM R13220 nr Mt Davies Bore, Tomkinson Range (26°10'S, 129°08'E), 18.x.1972; SAM R13221a-f 3 miles SW Mt Edwin, Mann Range (26°07'E, 129°56'E), 22.x.1972; SAM R28274-80, SAM R28289 nr Victory Well, Everard Range (27°03'S, 132°31'E), 25-26.viii.1987; SAM R28283-84 between Victory Well and Betty Well, Everard Range (27°03'S, 132°31'E), 26.viii.1987;

SAM R31772 2.4 km E Mimili (27°01'S, 132°44'E), 10.xii.1987; SAM R31773-4 19.2 km W Mimili (26°57'S, 132°32'E), 10.xii.1987; SAM R31791, SAM R35828 45.5 km SE Fregon (26°54'S, 132°24'E), 19.xii.1987; SAM R33940-2, SAM R33947-48, SAM R35829 Mimili (27°01'S, 132°43'E), 11.iv.1989; WAM R31768-80 Mt Lindsay, Birksgate Range (27°02'S, 129°53'E), viii.1968; WAM R44341-69 Mt Lindsay, Birksgate Range (27°02'S, 129°53'E), 1.ix.1972; WAM R44370-71 Mt Wooltarlinna, Birksgate Range (27°04'S, 129°51'E), 1.ix.1972; WAM R44385-87 Mt Kintore (26°34'S, 130°29'E), ix.1972; WAM R44341 Blackstone Mining Camp, Blackstone Range (26°01'S, 128°22'S), 29.viii.1972.

#### *C. vadrappa*

SAM R457 Farina (30°04'S, 138°17'E), 8.iv.1915; SAM R3764a-d Marree Picnic Ground (29°39'S, 138°04'E), 1.xi.1955; SAM R10959 East Painter Gorge (30°14'S, 139°22'E), 31.x.1969; SAM R12505 Yudnamutana (30°10'S, 139°17'E), 10.ix.1970; SAM R13547 Terrapinna Spring



(29°58' S, 139°40' E), 17.vi.1960; SAM R13943a-b Finnis Creek W Marree (29°38' S, 137°31' E), 10-15.i.1974; SAM R14481 Aroona Reservoir (30°35' S, 138°22' E), 15.i.1974; SAM R15098a-b Aroona Dam (30°35' S, 138°22' E), no date; SAM R15956a-d Mt Serle (30°32' S, 138°53' E), 10.iv.1977; SAM R16159 Mt Serle (30°31' S, 138°55' E), 4.ix.1977; SAM R16189a-b Termination Hill, 26km W Lyndhurst (30°15' S, 138°03' E), 8.x.1977; SAM R19284 10 miles W Arkaroola village (30°47' S, 138°30' E), 16.ii.1981; SAM R19884-5 15km W Copley (30°30' S, 138°25' E), 25.iv.1981; SAM R24430-31 W end Brachina Gorge, Flinders Ranges (31°21' S, 138°33' E), 20.viii.1983; SAM R24906-7 Grindells Hut, Gammon Ranges (30°28' S, 139°12' E), 25.xi-1.xii.1983; SAM R28098 5km N Copley (30°30' S, 138°25' E), 16.viii.1985; SAM R28625-6 Arkaroola (30°20' S, 139°22' E); SAM R29575 Marree Picnic Ground (29°39' S, 138°04' E), 23.viii.1985; SAM R30051-3 30.6km S Lyndhurst (30°32' S, 138°25' E), 21.ix.1985; SAM R30054 3.5km S Arkaroola (30°22' S, 139°27' E), 31.ix.1985; SAM R30999 32km S Lyndhurst (30°32' S, 138°25' E),

8.xi.1986; SAM R31002 Aroona Dam (30°35' S, 138°22' E), 23.viii.1986; SAM R31216 5.4km NW Copley (30°32' S, 138°25' E), 8.xi.1986; SAM R31219-22 Italowie Gap, Gammon Ranges (30°33' S, 139°10' E), 4-8.iv.1985.

## ACKNOWLEDGMENTS

A. Edwards and M. Hutchinson (SAM) and L. Smith (WAM) allowed access to specimens held in their care. S. Donnellan and J. Cornish provided Figures 1 and 2, respectively. Field work for this paper was funded in part by the Peter Rankin Trust Fund for Herpetology. C. M. Bull, M. Hutchinson and G. Witten made helpful comments on the manuscript.

## REFERENCES

- ALBERCH, P., GOULD, S. J., OSTER, G. F. & WAKE, D. B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* **5**: 296-317.
- COGGER, H. G. 1961. 'An investigation of the Australian members of the family Agamidae (Lacertilia) and their phylogenetic relationships'. Unpublished M.Sc. thesis, Sydney University.
- GIBBONS, J. R. H. & LILLYWHITE, H. B. 1981. Ecological segregation, colour matching, and speciation in lizards of the *Amphibolurus decresii* species complex (Lacertilia: Agamidae). *Ecology* **62**: 1573-1584.
- GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews* **41**: 587-640.
- HOUSTON, T. F. 1974. Revision of the *Amphibolurus decresii* complex (Lacertilia: Agamidae) of South Australia. *Transactions of the Royal Society of South Australia* **98**: 49-60.
- HOUSTON, T. F. 1978. 'Dragon Lizards and Goannas of South Australia'. South Australian Museum: Adelaide.
- HUXLEY, J. S. 1932. 'Problems of Relative Growth'. Dial: New York.
- NORUSIS, M. J. 1986. 'SPSS/PC+ Advanced Statistics'. SPSS: Chicago.
- REYMENT, R. A., BLACKITH, R. E. & CAMPBELL, N. A. 1984. 'Multivariate Morphometrics'. 2nd Edn. Academic Press: London.
- SOKOL, R. R. & ROHLF, F. J. 1981. 'Biometry'. 2nd Edn. W. H. Freeman: San Francisco.
- STORR, G. M. 1981. Three new agamid lizards from Western Australia. *Records of the Western Australian Museum* **8**: 599-607.
- STORR, G. M., SMITH, L. A. & JOHNSTONE, R. E. 1983. 'Lizards of Western Australia. II. Dragons and Monitors'. Western Australian Museum: Perth.
- WARBURG, M. R. 1966. Water economy of several Australian geckos, agamids and skinks. *Copeia* **1966**: 230-235.
- WHITE, J. 1979. The road to Mokari. *Herpetofauna* **11**: 13-16.
- WITTEN, G. J. 1982. 'Comparative morphology and karyology of the Australian members of the family Agamidae and their phylogenetic implications'. Unpublished Ph.D. thesis, Sydney University.
- WITTEN, G. 1985. Relative growth in Australian Agamid lizards: adaptation and evolution. *Australian Journal of Zoology* **33**: 349-362.
- ZAR, J. H. 1974. 'Biostatistical Analysis'. Prentice-Hall Inc.: New Jersey.

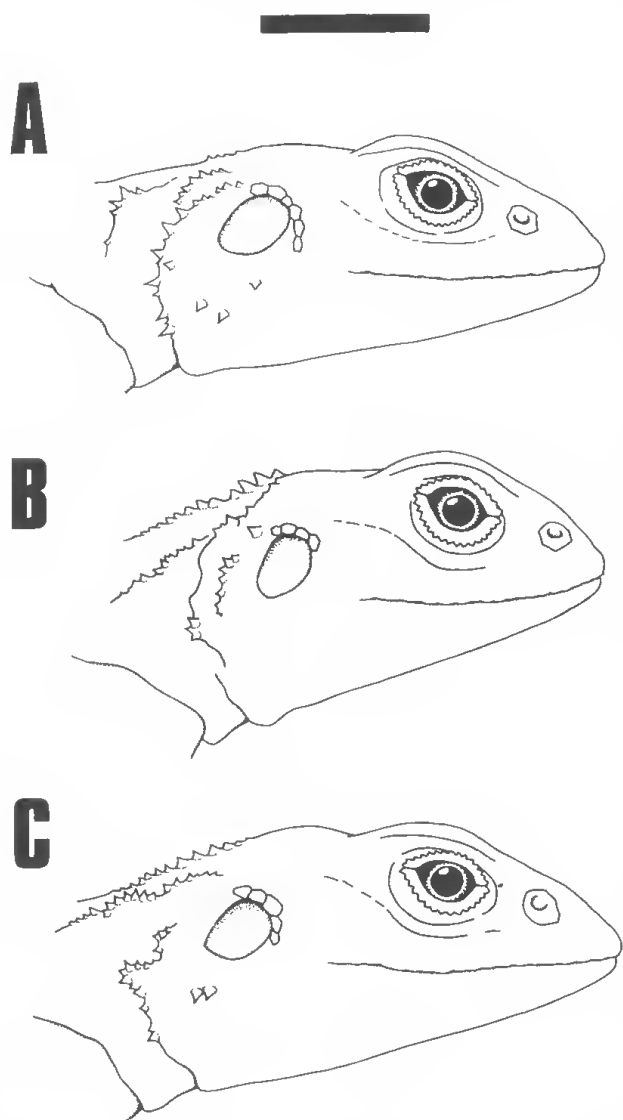


FIGURE 5. Lateral views of the heads of adult male (A) *Ctenophorus rufescens* (SAM R13221c), (B) *Ctenophorus tjantjalka* (SAM R17934a) and (C) *C. vadnappa* (SAM R16189a). Scale bar = 10mm.